

# STUDIES IN *GLANDULARIA* (VERBENACEAE): THE *GLANDULARIA QUADRANGULATA* COMPLEX

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## ABSTRACT

This paper responds to Turner's inclusion of *Glandularia verecunda* and *G. racemosa* into *G. quadrangulata*. The latter has distinctive terminal appendages on the nutlets and the pericarp flares outward at the base; *G. verecunda*, is very similar vegetatively, has similar nutlets, but they lack the distinctive terminal appendage. Pollen/ovule ratios indicate that both taxa are facultative autogamous and both taxa have distinct ranges with limited areas of sympatry. No intermediates are known, and intermediate characteristics may not exist. They also differ in their flavonoid compliments supporting their recognition as distinct species. *Glandularia racemosa*, with larger corollas, a different nutlet type, and leaf structure, is a hexaploid (not tetraploid as in the other taxa) and represents a separate group within the genus and should not have been submerged into *G. quadrangulata*.

## RESUMEN

Este artículo responde a la inclusión de Turner de *Glandularia verecunda* y *G. racemosa* en *G. quadrangulata*. Esta última tiene apéndices terminales distintivos en las núculas y el pericarpio se acampana hacia el exterior en la base; *G. verecunda*, es muy similar vegetativamente, tiene núculas similares, pero le falta el apéndice terminal distintivo. La relación polen/óvulos indica que ambos taxa son autógamos facultativos y ambos taxa tienen diferente distribución con áreas de simpatria limitada. No se conocen intermedios, y los caracteres intermedios puede que no existan. También se diferencian en su dotación de flavonoides que apoyan su reconocimiento como especies distintas. *Glandularia racemosa*, con corolas más grandes, un tipo diferente de núcula, y estructura de la hoja, es un hexaploide (no tetraploide como en los otros taxa) y representa un grupo separado en el género y no debería haber sido incluida en *G. quadrangulata*.

## INTRODUCTION

Turner (1998) presented a new classification *Glandularia quadrangulata* (Heller) Umber submerging both *G. verecunda* Umber and *G. racemosa* (Eggert) Umber into *G. quadrangulata*. All three taxa are similar vegetatively. They are low-growing, branched, hairy, usually perennial herbs with broad, distally dissected leaves and have small, inconspicuous flowers with corolla limbs only 2.5–9 mm wide. Turner (1998) however, failed to take into consideration basic differences in nutlet structure, ploidy levels, and breeding systems of these taxa that support a different classification.

## MATERIALS AND METHODS

The data presented here are based on empirical observations on specimens from the TEX-LL, SRSC herbaria. Direct counts of pollen grains were made from



unopened buds that were softened by boiling; the four anthers were opened directly on microscope slide.

#### RESULTS AND DISCUSSION

*Nutlet structure.*—Nutlets of *G. quadrangulata* are the most distinctive (Fig. 1 D). The nutlets are 3.3–4.2 mm long, the central bodies are slender, 0.55–0.65 mm wide, at the base and the outer pericarp wall greatly expands and flares outward to 1.2–1.6 mm in width. At the inner tip they have a large, thin, somewhat concave, ovate appendage 1.0–1.3 mm long. The inner or commissural surface of the nutlet is cream-white and covered with distinct papillate-aculeate excrescences. The commissural surface is nearly as wide as the nutlet in the central portion and extends to the top of the ovate appendage. The outer pericarp walls, as in most glandularias, are black, with a broad reticulate, raised pattern that extends from the tip about half way down the nutlets where it disorganizes into a series of vertical striae that extend to the nutlet base. The quartet of nutlets are so arranged that the flared bases expand over the receptacle and the distal appendages form a valvate dome over the developing nutlets through which the style extends from the tip of the united appendages. When the nutlets separate, they leave no distinctive receptacular rim.

The fruits of *Glandularia verecunda* are similar to those of *G. quadrangulata* except they lack the conspicuous terminal appendage (Fig. 1 H). They are (2.6–)2.8–3.2(–3.3) mm long, and the central body is also slender, 0.5–0.65 mm wide. The outer pericarp also abruptly flares out at the base to a width of 1.0–1.3 mm although this characteristic is not present in immature fruit. Again the inner whitish commissural face is nearly as wide as the central nutlet itself. The aculeate surface continues to the distal portion of the nutlet where its distal margin is rather truncated, sometimes retuse, marked by small horizontal beak that extends inward. The horizontal beak may be homologous to the much-expanded vertical beak in *G. quadrangulata*. In their broadly flared base and slender body, the broad commissural face of the nutlets are identical to those of *G. quadrangulata*.

Nutlets with similar slender bodies and greatly expanded bases occur in a small group of North American *Glandularia*, namely *G. polyantha* Umber, *G. delticola* (Small) Umber, and in two other taxa that also have greatly expanded air spaces in the adaxial portion of the nutlet: *G. tumidula* (Perry) Umber, and *G. brachyrhynchos* Nesom & Vorobik. Of note, the distinctive nutlet appendage is not unique to *G. quadrangulata* as it also occurs in species of southern South America (Uruguay, Brazil and Argentina) where *Glandularia tenera* (Spreng) Cabrera has an appendage similar to that of *G. quadrangulata* and *G. pulchella* (Sweet) Tronc. has a shorter, less-developed appendage. *Glandularia pulchella* is adventive in the United States from Florida into Texas and in northeastern



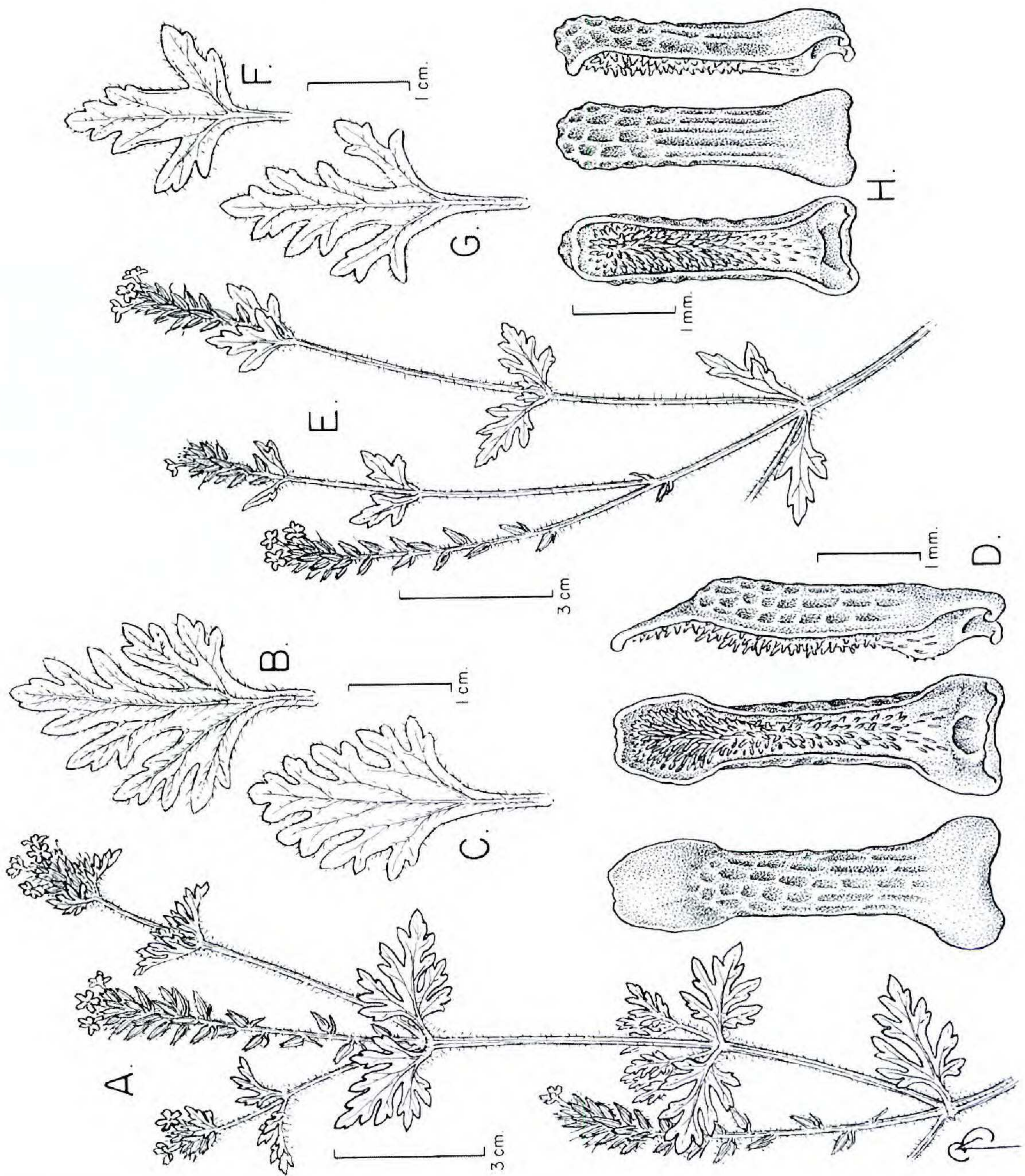


FIG. 1. *Glandularia quadrangulata* and *G. verecunda*. A–D. *G. quadrangulata*. A. Stem, showing leaves and inflorescences (Lundell 9790, LL); B. Leaf, adaxial view, (Lundell 9790, LL); C.—Leaf, adaxial view (Turner 21-112, TEX); D. Mature nutlets showing the distinctive ovate terminal appendage and broadly flaring basal pericarp as seen in abaxial view (left) showing outer reticulate pattern, (note broad expansion of nutlet base), in adaxial view (central) showing aculeate inner commissural surface nearly as wide as the nutlet, and in lateral view (right) showing adaxial location of the terminal appendage (all Carr 15923, TEX). E–H. *G. verecunda*. E. Stem, showing leaves and inflorescence (Strohmeyer s.n., TEX); F. Leaf, adaxial view (Strohmeyer s.n., TEX); G. Leaf, adaxial view (Henrickson 22775, TEX); H. Mature nutlets showing lack of terminal appendage and broad nutlet base in adaxial view (left) with aculeate commissural face nearly as wide as the mid-nutlet and continuing to near the nutlet tip, abaxial view (central) showing abaxial nutlet surface (note: reticulate pattern near the tip that breaks apart below into parallel lines below), and lateral view (right) showing the small beak-like projection at the tip (all Bruno & Peña 38, TEX). Magnifications as indicated.



Mexico; most plants show moderate appendages, in some plants they are poorly developed, shorter and more perpendicular to the nutlet axis. Nutlets of both species are illustrated in Burkart and Troncoso (1979).

The nutlets of *Glandularia racemosa*, however, are strongly different and are of a type widely occurring through most North American *Glandularia* (Fig. 2 I). The body of the nutlets are (2.0–)2.2–2.6(–2.8) mm long, slightly broader, the basal pericarps are only slightly expanded and the nutlets are rounded at the tip. Furthermore the whitish aculeate or otherwise marked commissural surfaces are much narrower than the width of the nutlets (often 0.25–0.3(–0.35) mm wide, with the nutlet being (0.55–)0.6–0.77 mm wide), and this whitish commissural surfaces extends to within 0.2–0.4 mm of the dome-like nutlet tips where they are distinctly rounded, not truncated or retuse. The blackened pericarp, however, has a similar raised reticulate pattern in the distal half that disorganizes into a series of vertical striae as in the other two species.

*Cytology*.—Umber (1977, 1979) presents chromosome counts for the three taxa. Both *Glandularia quadrangulata* and *G. verecunda* are tetraploid with  $n = 10$ . *Glandularia racemosa* in contrast, is hexaploid with  $n = 15$ . An older count by Dermen (1936) also shows hexaploidy for *G. racemosa* ( $2n = 30$ ). This would not support submersion of *G. racemosa* into *G. quadrangulata*. Lewis and Oliver (1961) report  $n = 10$  (tetraploid) for *G. racemosa* based on a Lewis & Oliver 5416 collection from Coahuila, Mexico, however, Umber (1977) correctly notes this collection is *G. verecunda*, not *G. racemosa*.

*Phytochemistry*.—Umber (1977) notes that the west Texas populations of *Glandularia verecunda* and *G. racemosa* are similar in their flavanoids both producing 7-0-gentiobiosides and 7-0-sophorosides of apigenin, luteolin and chrysoeriol, while six south-Texas samples *G. quadrangulata* produced only 7-0-gentiobiosides (but not 7-0-sophorosides) of apigenin (its dominant flavonoid), with only trace amounts of 7-0-gentiobiosides of luteolin and chrysoeriol. The south Texas sample of *G. verecunda*, however, also produced only 7-0-gentiobiosides of apigenin, luteolin and chrysoeriol as in *G. quadrangulata*.

*Biogeography*.—Each of these three taxa have distinct ranges: *Glandularia quadrangulata* occurs from south-central Texas west to the Pecos River and to the border region of Mexico (Fig. 3). *Glandularia verecunda* occurs in trans-Pecos Texas, scattered in southern Texas, and continues south into Mexico in eastern Chihuahua, eastern Coahuila, south to near Monterrey in Nuevo León. *Glandularia racemosa* is restricted to trans-Pecos Texas (Fig. 3).

*Breeding systems*.—Flowers in both *Glandularia quadrangulata* and *G. verecunda* are very small having white to lavender corollas with very slender tubes 5.2–6.5 mm in length and limbs 2.5–5.2 mm in diameter. Within the tube, as in all glandularias, the style is initially situated between the two pair of introrse anthers among a series of downward-pointing stiff hairs (see Fig. 2 E–H).



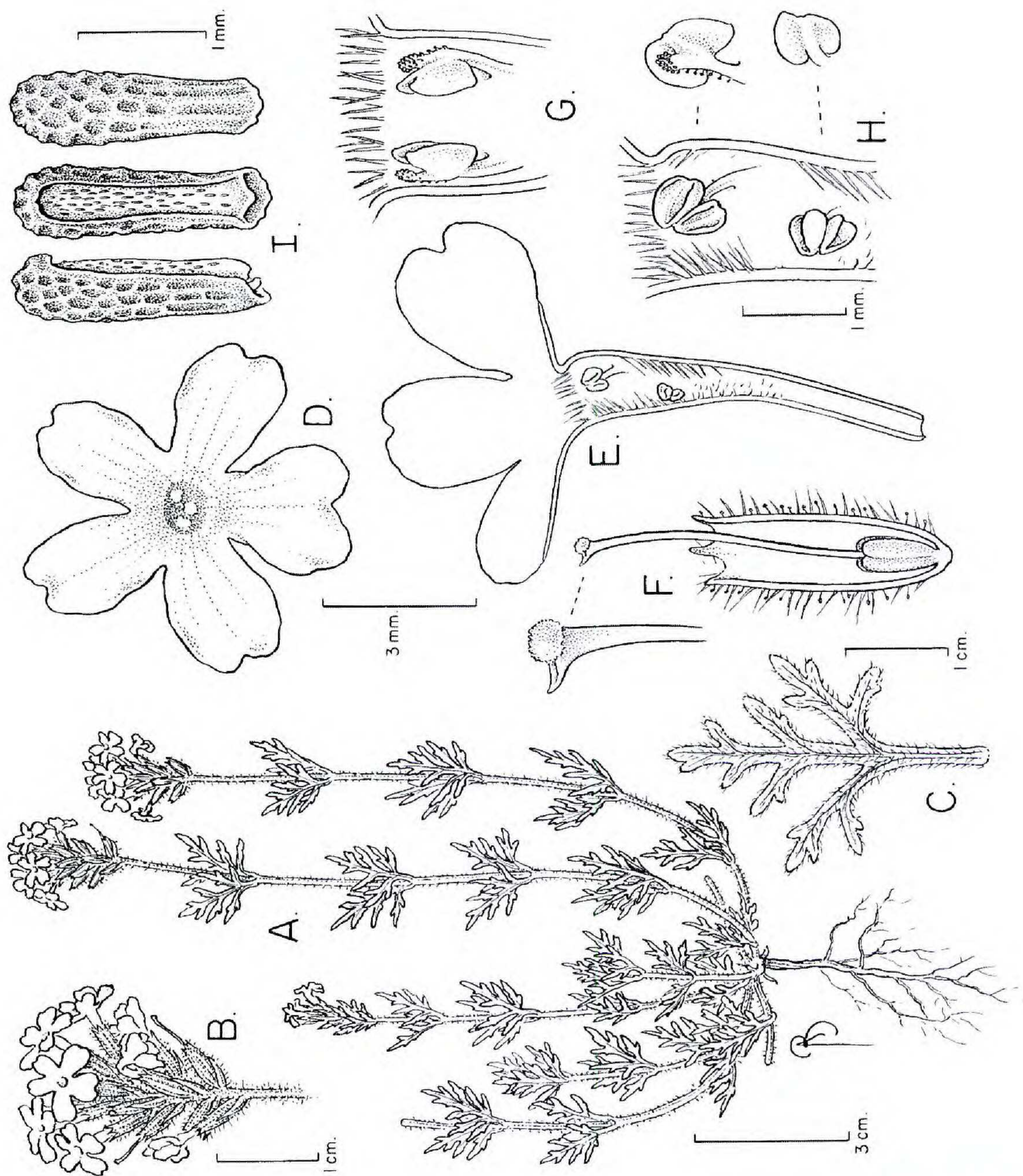


FIG. 2. *Glandularia racemosa*. **A.** Growth habit of young plant showing erect stems and terminal inflorescences (Turner 21-212, TEX); **B.** Inflorescence with corollas; (Turner 21-212, TEX); **C.** Leaf, adaxial view (Turner 97-28, TEX); **D.-H.** Floral structure (from re-expanded flowers of Turner 21-74 TEX and others) **D.** Corolla, face view, showing larger, more emarginate abaxial corolla limb, and relatively smaller adaxial limbs; **E.** Medial section of corolla, showing separation of distal abaxial and more proximal adaxial stamens, the hairs at the corolla tube throat are moniliform, those of the tube are stiffer, more subulate; **F.** Medial section of calyx, showing ovary, style and stigma (offset). The stigma lies between the two pairs of stamens; **G.** Distal stamens, showing lateral glandular connective appendages; **H.** Distal and proximal stamens and associated hairs (note the connective appendage on the distal stamen—offset); **I.** Mature nutlets showing narrow nutlet base and relatively narrow commissural face, lateral view (left) showing reticulate abaxial surface, adaxial view (central) showing the narrow commissural face, and abaxial view (right) showing the reticulate surface pattern that is less organized below (Warnock 46135, TEX). Magnifications as indicated. Scale in D, holds for D, E, and F.



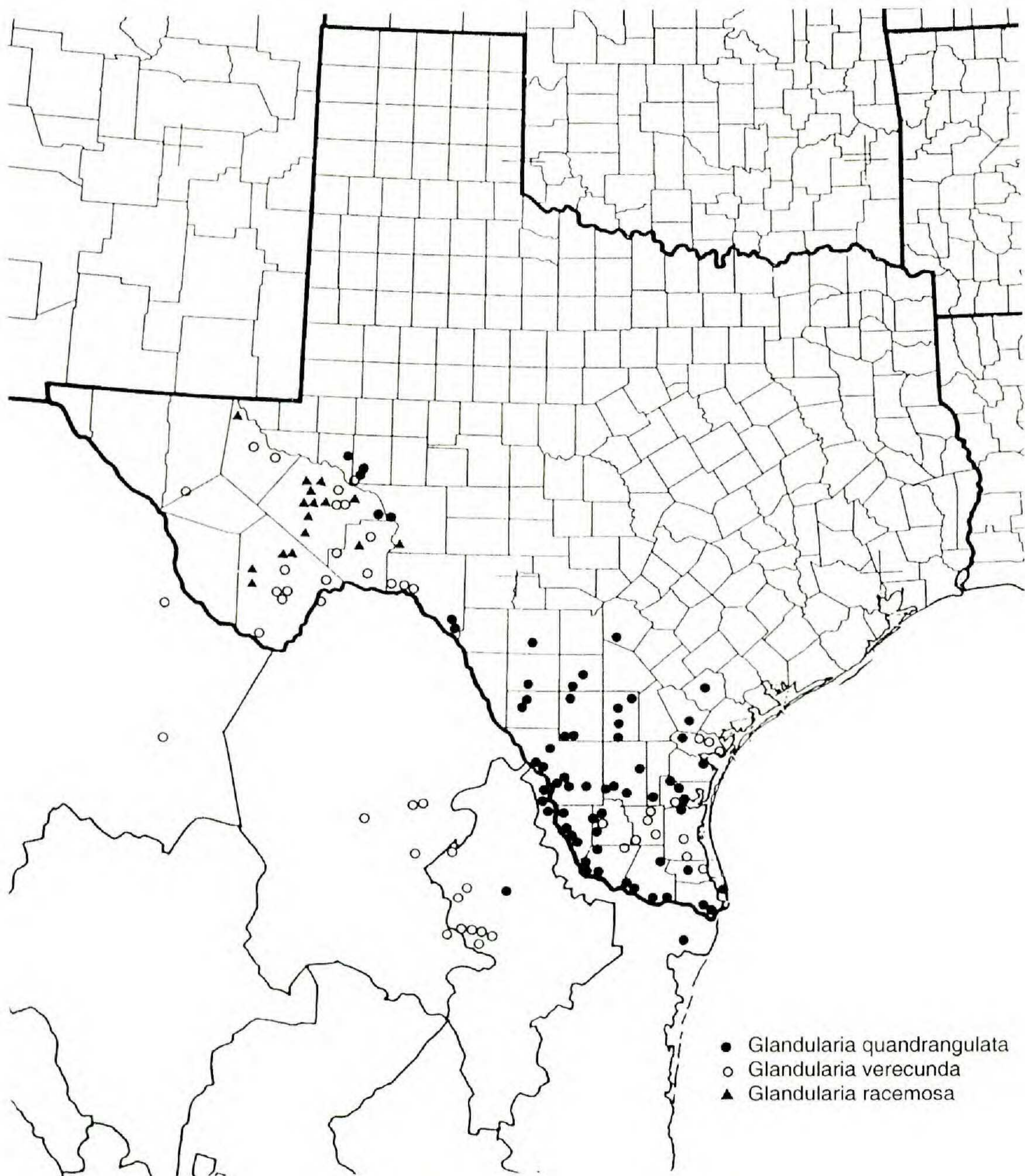


FIG. 3. Distributions of *G. quadrangulata* (solid circles), *G. verecunda* (hollow circles) and *G. racemosa* (solid triangles) in Texas and Mexico, from collections at TEX-LL and SRSC.

The basal two anthers are 0.3–0.6 mm long, with filaments to 0.3 mm long and contain fewer pollen grains than present in the slightly larger distal pair of anthers that are 0.4–0.8 mm long with filaments 0.3 mm long. As the flower matures, the style elongates pushing the stigma across the distal pair of anthers where pollen easily contacts the stigma. Unless some self-incompatibility factors are at work, autogamy (inbreeding) is certainly possible. Regarding self incompatibility, I have observed that even isolated plants of *G. quadrangulata* set a full complement of nutlets, and in most herbarium specimens, the plants have full



fruit set, leading me to believe that there is no self incompatibility involved in the reproduction of the taxon.

Cruden (1977) noted that pollen-ovule ratios can be used as an indicator of the breeding system in flowering plants. In his study, he indicated average pollen/ovule ratios of 4.7 (range 3–7) for cleistogamous taxa; 27.7 (range 18–30) for obligate autogamous taxa; 168.5 (range 76–396) for facultative autogamous taxa; 796.6 (range 160–2,558) for facultative xenogamous (outbreeding) taxa; and 5859 (range 1,648–16,807) for obligate xenogamous taxa using his outcrossing index as a relative measure of inbreeding vs. outcrossing.

*Glandularia* species in North America differ strongly in corolla size, with larger flowers having larger anthers with more pollen. I measured pollen grain numbers per flower and correlated that with overall flower size (using maximum expanded diameter of the corolla limb as a gross measurement of corolla size) in several species of *Glandularia*. I found that plants with corolla limbs 9–13 mm in diameter had 2168–2677 pollen grains (5 counts) (average 2344 per flower, 586 pollen grains per ovule—four ovules per ovary). Flowers with corolla limbs 4–7 mm in diameter had 956–1410 pollen grains per flower (8 counts) (average 1275 per flower, 318 pollens per ovule) and those with corolla limbs 2–4 mm in diameter, had 580–1149 pollen grains (7 counts) (average 748 per flower, 187 pollen grains per ovule) indicating that most *Glandularia* were in the range of facultative autogamous. As noted above, the stigma is also produced in close association with the anthers in the distal corolla tube. For the species here in question, I found in four collections of *G. quadrangulata*, 580, 626, 615, 706 pollen per flower (mean of 157 per ovule—4 ovules per flower), (wetted corolla limb diameters 2.5, 2.5, 2.7, 2.5 mm respectively—see Table 1); for *G. verecunda* 1149, 870, 740, 692, pollen per flowers (mean of 218 per ovule), (corolla limb diameters of 2.5, 3.5, 5.2, 3.5 mm) and *G. racemosa* 2184, 2125, 1728, 1803 per flower (mean of 490 per ovule), (corolla limb diameters of 9.0, 8.5, 8.0, 7.8 mm). This would imply that the taxa, at least for *G. quadrangulata* and *G. verecunda*, are in the range of facultative autogamous taxa and *G. racemosa* is in the facultative xenogamous range.

Also, most plants, even isolated plants, exhibit full or nearly full fruit set. Ueber, (pers. comm.) notes that in many *Glandularia* species, greenhouse grown plants produced full fruit set, in some species you had to push the flowering branches back and forth, similar to a wind action, to insure good fruit set. Even the few, widely isolated specimens of *G. quadrangulata* I observed in Kleberg Co., Texas, all had near complete fruit maturation. Though Ueber 1977 notes that some populations of his *G. bipinnatifida* have low fruit set, indicating the possibility of local self incompatibility. My conclusion is that *G. quadrangulata* and *G. verecunda* are capable of reproducing by autogamy, and that self incompatibility does not restrict fruit set, so that even if they occur in sympatric populations, gene exchange between them may be limited and inci-



TABLE 1. Pollen/ovule ratios of *Glandularia* species.

	<b>Total pollen per fl.</b>	<b>p/o ratio</b>	<b>Corolla diameter</b>
<b><i>Glandularia quadrangulata</i></b>			
<i>Turner 97-01</i> Crockett Co., Tex.	580	145	2.5
<i>W.R. Carr 11723</i> McMullen Co., Tex.	615	153	2.5
<i>Williges 359</i> San Patricio Co., Tex.	626	156	2.7
<i>V. Villarreal</i> Kleberg Co., Tex.	706	176	2.5
	Average 157		
<b><i>Glandularia verecunda</i></b>			
<i>Correll 20699</i> Brewster Co., Tex.	1149	287	2.5
<i>Powell, Turner &amp; Sikes</i> Ojinaga, Chih., Mex.	870	217	3.5
<i>Turner 97-86</i> Terrell Co., Tex.	780	195	5.2
<i>Lundell &amp; Lundell 10071</i> Brooks Co., Tex.	692	173	3.5
	Average 218		
<b><i>Glandularia racemosa</i></b>			
<i>Turner 97-28</i> Pecos Co., Tex.	2184	546	9.0
<i>Turner 97-212</i> Culberson Co., Tex.	2125	531	8.5
<i>Turner 97-76</i> Brewster Co., Tex.	1728	432	8.0
<i>Tharp &amp; Havard 49359</i> Pecos Co., Tex.	1803	451	7.8
	Average 490		

dental. Certainly both taxa produce flowers with small corolla tubes that may be attractive to long-tongued flies (J. Neff, pers. comm.) but are certainly capable of self pollination.

*Classification.*—The relationship of *Glandularia racemosa* to the other two taxa, is very clear. While *G. racemosa* is somewhat vegetatively similar to both *G. quadrangulata* and *G. verecunda*, the leaves of *G. racemosa* are more deeply divided into linear segments (except in some large, perhaps shaded leaves of rapidly-growing specimens), its growth habit is different, initially briefly decumbent at the base with erect-ascending stems, but with age it becomes more spreading. Furthermore the fruits of *G. racemosa* are completely different as



discussed above and are of a type found in most North American *Glandularia*. Also both *G. quadrangulata* and *G. verecunda* are tetraploid ( $n = 10$ ), while *G. racemosa* is hexaploid ( $n = 15$ ). In addition the corollas of *G. racemosa* are larger [(5.5-)6-8(-9.0) mm in limb diameter] than those of *G. quadrangulata* [(2.0-)2.5-3.5(-4.5) mm diameter] and *G. verecunda* [3.2-4.5(-5.5) mm diameter]. Corolla limbs of *G. racemosa* are also usually white in color [rarely tinged with blue—which Umber (1977, 1979) considers indication of introgression with *G. bipinnatifida*], while those of *G. quadrangulata* and *G. verecunda* are more commonly lavender, only occasionally white in color. It is apparent that *G. racemosa* is not a taxonomic synonym of the *G. quadrangulata-verecunda* group and is a distinct, endemic species in trans-Pecos Texas. I find no support for Turner's inclusion of *G. racemosa* into his concept of *G. quadrangulata* other than gross vegetative similarity.

While *Glandularia quadrangulata* and *G. verecunda* have largely allopatric ranges, mixed populations occur near the Pecos River and in southern Texas. In fact there are three herbarium collections at TEX-LL that contain material of both taxa: two from Upton County, Texas, 3.1 miles east of McCamey, 21 Apr 1999, Turner 99-179 and 99-200 (TEX) and one from southern Texas, Kleberg Co., Texas; Hwy. 77, 2 mi W of Riviera, 15 Mar 1965, Ramirez & Cardenas 78 (TEX). An additional pair of specimens from SRSC (Brewster Co., Texas, sandy soil along the Rio Grande at Boquillas, 10 May 1933, H.T. Fletcher 1224 (*G. quadrangulata*) 1226 (*G. verecunda*) were apparently collected in the same area. In vestiture, leaf size and shape the two taxa are very similar, if not identical.

The overall similarity and occasional sympatry of *Glandularia quadrangulata* and *G. verecunda* caused Turner (1998) to conclude that *G. verecunda* was only a ex-appendiculate form of *V. quadrangulata* unworthy of formal nomenclatural recognition although he presented no evidence of introgression. But we must ask, what characteristics would be expected in hybrids? Would they have intermediate appendages or no appendage at all and be identical with *G. verecunda*?

No plants have ever been discovered in nature with nutlets intermediate in structure between those of *G. quadrangulata* and *G. verecunda*. All plants either have nutlets with or without the distinctive distal appendage. Furthermore, no artificial hybridization has been done to determine the condition that would be expressed in a hybrid. The pattern found with *G. quadrangulata* and *G. verecunda* presents an interesting conundrum. Are the two taxa merely forms of one other, as Turner espouses, separated by only a single character that is either expressed or not, so that hybrids would be identical to one taxon or another? Or are they two separate species that do not or seldom hybridize? Or should they be recognized at least at the infraspecific level?

It remains that the two taxa are nearly identical vegetatively and florally except for the distal nutlet appendage on *G. quadrangulata*. I concede that the



two are most-closely related or sister taxa; to think otherwise would be difficult to defend. But there seems to be a stability in their lineages as indicated by their respective large and mostly independent geographical ranges.

The genetic basis of the nutlet-appendage character is not known. If it is a simple Mendelian trait, it would appear not to have a high mutation rate. If the appendaged nutlet type in *Glandularia quadrangulata* were pleisomorphic and dominant state (i.e., AA, or Aa) and the non-appendaged nutlets represented a loss of this character (i.e., aa), then once a mutation (a) forms, or once hybridization occurs, one would expect the heterozygotic plants to form seeds at a 1:2:1 genotypic ratio (1AA:2Aa:1aa), a phenotypic ratio of 3 appendaged to 1 non-appendaged character state while the homozygous plants would breed true over successive generations. The same pattern would be expected if the appendage were a recessive character state. Whether this is occurring in certain localities is unknown. But it remains that large geographical regions are occupied by plants with either appendaged or non-appendaged nutlets indicating a low rate of mutation or hybridization. If mutation rates were higher, or hybridization more frequent, homozygous recessive traits would be expected throughout the dominant-trait populations.

Turner (1989) has treated the two taxa as unnamed forms, relegating Umber's *G. verecunda* to obscurity. But if the two taxa are facultative autogamous, they could very well become sympatric without mixing and thus behave much like species. Likewise if they are allopatric, and mutation rate is very low, again they would breed true to form and behave as species. To relegate the two taxa to unnamed forma, is not reflective of the conditions observed in nature. In typical forma, the homozygous recessive character states usually occur scattered in some or many populations, their frequency reflecting the frequency of the recessive trait. These two taxa behave more like species. They each have broad geographical ranges. The distinguishing character state is conspicuous. There is a possibility that in some populations, where both taxa are present, they may have introgressed and mixed populations are being produced through recombination. But as there is no intermediate character state, the populations would appear to be consisting of two sympatric separate taxa. If they actually are interbreeding, there would be no way to tell except by growing the nutlets out from these mixed populations to see if they breed true to form. I have visited two populations where the two taxa are sympatric, west of Riviera, in Kleberg Co., Texas and west of McCamby, in Upton Co., Texas in the late spring of 2001. In the former the roadside populations are largely being replaced by Bermuda Grass, but some nutlets were collected from scattered specimens of *G. quadrangulata*. In the Upton County populations, no plants were found presumably due to local rainfall conditions.

Of the three nomenclatural possibilities: (1) being inconsequential forms of each other; (2) being geographical subunits of a species, i.e., subspecies or



varieties of one species; or (3) being separate species that merely co-occur in some areas. I consider that the first choice is least supportable. Mixed populations are few, no plants with intermediate fruit conditions are known to exist, plants with the two fruit types occur in broad, somewhat discrete geographical ranges. This treatment would ignore the pattern of variation as it would not be reflected in the nomenclature. One could argue, just as strongly, that the two taxa are distinct species that are very similar vegetatively that can co-occur without interbreeding as no intermediates have ever been found. But the lack of interbreeding may be based in autogamy more than some other type of isolating mechanism.

If there was evidence of interbreeding, they the two taxa could be recognized at the infraspecific level. But this does not exist. Therefore the two taxa will here be recognized as distinct species.

**Glandularia quadrangulata** (Heller) Umber (**Fig. 1 A–D**). BASIONYM: *Verbena quadrangulata* Heller, Contr. Herb. Franklin Marshall Coll. 1:84, pl. 6, 1895. TYPE: U.S.A. TEXAS. NUECES CO.: Corpus Christi, 5 Mar 1894, *Heller 1388* (HOLOTYPE: (in part) NY; ISOTYPES: GH, MO).

*Verbena pumila* f. *albiflora* Standl., Field. Mus. Publ. Bot. 4: 256, 1929. TYPE: U.S.A. TEXAS. BEXAR CO.: San Antonio, *L.E. Pagel 2208* (HOLOTYPE: F).

Weak-stemmed annuals 0.5–2 dm tall; stems several from the base, 1–3(–7) dm long, initially briefly decumbent, erect above, with age spreading, decumbent, ascending distally, the internodes (1.2–)2–5(–11) cm long, green to tan, sometimes purple with age, grooved on two sides when young, this obscured when larger, moderately (to strongly below inflorescence) hirtellous to pilose with slender, tapering erect, mostly straight hairs 0.2–1.2(–1.8) mm long, sometimes with stipitate glands to 0.2 mm long. Leaves ovate to ovate-rhombic in outline (12–)15–25(–38) mm long, (8.5–)10–20(–30) mm wide, usually much shorter than the internodes, with petioles 2–11 mm long, the blades 3–5 cleft about half, two-thirds way to the midrib, the clefts entire to few to strongly toothed and lobed, usually moreso on the outer margins, ultimately the leaf with 7–22 oblong to oblong-obovate, obtuse-rounded, sometimes acute lobes 1–2.5(–3.5) mm wide, the blades flat to usually somewhat concave and with impressed primary-secondary veins above, with rather stiff, tapering unicellular hairs 0.3–0.8(–1.1) mm long on both surfaces, these generally dispersed and ascending above, mostly along the yellowish raised veins and the slightly revolute margins (or ± uniformly scattered) beneath, those of the upper surface sometimes pustulate based. Spikes terminal on all branches, initially crowded with a short peduncle, 9–11 mm wide, with age the inflorescence axis elongating below, and the lowermost developing fruit becoming increasingly more remote, until separated by 5–7 mm along the axis, the inflorescences then extending 4–13 cm long with a peduncle to 5 cm long, the spike rachis ± densely pilose with hairs to 1.8 mm long; bracts ascending, linear-lanceolate, 3.2–5.5 mm long, hirsute along margins and



midvein with hairs 0.2–1.6 mm long, 59–79 percent as long as the calyx; calyces initially 5.0–6.5 mm long, membranous between the 5 green veins, hirtellous and hirsute with hairs 0.2–1.2 mm long, without or without stipitate glands, the lobes unequal, 0.4–0.8 mm long, green or purple tipped, in fruit the calyces expanding around the nutlet becoming strongly truncated and to 2.5 mm broad at the base; corollas salverform, the slender tubes 5.2–6.6 mm long, 0.4–0.6 mm wide at the throat, the limbs white to lavender, (2.0–)2.5–3.5(–4.5) mm wide, the 5 lobes all retuse, or the upper two lobes not retuse, 1.0–1.2 mm long, 0.5–1.3 mm wide; the tube orifice with gold-white moniliform hairs to 0.5 mm long; distal anthers 0.4–0.5 mm long, the anther gland obscure, with filaments 0.3 mm long, the proximal anthers 0.3 mm long, with filaments 0.2 mm long; style 4–5.2 mm long. Mature fruit (3.3–)3.5–4.2 mm long, the distal, adaxial, obtuse, ovate appendage 1.0–1.4 mm long, 0.8–1.0 mm wide, the central body cylindrical, 0.55–0.65 mm wide, the cream-colored commissural face 0.38–0.55 mm wide, this extending throughout the distal appendage, strongly aculeate with papillae to 0.25 mm long, the basal pericarp expanded, forming a hollow chamber to 1.0–1.6 mm wide, the outer pericarp black, shallowly reticulate in the distal half, the reticulate pattern disorganizing into vertical striae in the lower half, the post-dehiscent receptacle small, not whitish or whitish-cream.

The species is characterized by its moderate to strongly incised leaves that are relatively broad along the midvein (often cleft to only 1/3 to total width), by the small corollas, and by distinctive nutlets that have narrow central bodies, with the pericarp greatly expanding at the base, with a conspicuous, spoon-like appendage nearly 1 mm high at the tip, with the commissural face nearly as wide as the mid nutlet, continuing into the distal appendage. Relationships of the species may also lie with two other species in North America that have similar nutlets with broad commissural faces: *Glandularia shrevei* (Moldenke) Umber and possibly *Glandularia bajacalifornica* (Moldenke) Umber (Umber 1979).

Widespread in southern Texas and closely adjacent Mexico also in west Texas near the Pecos River (Fig. 3), in limestone, caliche, gravelly to sandy, clayish soils in coastal prairie, thorn scrub, in cis-Pecos Texas in desertic scrub, often roadsides, open areas, 10 to 1000 m, flowering late February to April.

***Glandularia verecunda*** Umber, Syst. Bot. 4:99. 1979. (**Fig. 1 E–H**). TYPE: U.S.A. TEXAS. REEVES CO.: 2.5 mi E of Toyah, R. & J. Umber 379 (HOLOTYPE: GH; ISOTYPES: TEX!, NY).

*Verbena pumila* f. *albida* Moldenke, Phytologia 9:188. 1963. TYPE: U.S.A. TEXAS. KENEDY CO.: at the edge of Kenedy Co., Highway 96 at the Willacy Co. line, 18 Apr 1941, Runyon 2499 (HOLOTYPE: NY; ISOTYPE: TEX!).

Vegetatively similar to *G. quadrangulata* but the leaves more ovate to obovate in outline (12–)15–25(–42) mm long, (9.5–)10–20(–25) mm wide, with petioles 4–8 mm long, the lateral clefts more often entire or with fewer lateral teeth-lobes, and the hairs more often with pustulate bases. Inflorescence bracts lin-



ear-lanceolate to lanceolate, 3.2–6.5 mm long, 49–87 percent as long as the calyces; calyces 5.5–7.0 mm long, the lobes, 0.4–1.1 mm long, in fruit the calyces to 1.7–2.5 mm broad at the base; corolla tubes 5.5–7.0 mm long, 0.5–0.9 mm wide, the limbs white to lavender, 3.2–4.5(–5.5) mm wide, the 5 lobes all retuse, or the upper two lobes not retuse, 1.4–1.8 mm long, 0.8–2.0 mm wide; the distal anthers 0.6–0.8 mm long, with filaments 0.5–0.7 mm long, the proximal anthers 0.4–0.6 mm long, with filaments 0.2 mm long; styles 5.0–5.2 mm long. Mature nutlets (2.6–)2.8–3.3 mm long, lacking a terminal appendage, the central body 0.5–0.6(–0.65) mm wide, the cream-colored commissural face 0.35–0.5 mm wide, this extending to within 0.05–0.2 of the tip of the fruit, the distal commissural surface truncate or slightly retuse, the inner tip of the fruit with a short inward pointing, tapering, horizontal appendage to 0.2 mm long, the commissural face aculeate with papillae to 0.15 mm long, the basal pericarp expanded, forming a hollow chamber to 1.0–1.3 mm wide, the post-dehiscent receptacle 1.0–1.2 mm wide, whitish-cream in color.

South Texas and trans-Pecos Texas south into eastern Chihuahua, also eastern Coahuila and adjacent Nuevo León (Fig. 3) on calcareous and limestone derived clays, sandy soils, grasslands, thorn scrub, to *Larrea*, *Acacia*, *Hectia* scrub, also disturbed flats, roadsides, milpas; 5–800 m elevation; flowering, March through May, also in Fall with rains.

The taxon is vegetatively similar to that of *G. quadrangulata* has less strong cleft leaves, slightly larger corollas, anthers, and similar nutlets that, however, lack the distinctive distal appendage.

**Glandularia racemosa** (Eggert) Umber, Syst. Bot. 4:99. 1979. (**Fig. 2**). *Verbena racemosa* Eggert, Torreyia 2:123. 1902. TYPE: U.S.A. TEXAS. EL PASO (now Hudspeth) CO.: low sandy valley, Sierra Blanca, 15 May 1901, H.K.D. Eggert s.n. (HOLOTYPE: NY; ISOTYPES: GH, MO).

*Verbena pulchella* Greene, Pittonia 5:136. 1903. TYPE: U.S.A. TEXAS. JEFF DAVIS CO.: Foothills of the Davis Mountains, Tracy & Earl 106a (HOLOTYPE: ND-G?; ISOTYPES: NY, GH).

Usually thick-stemmed annuals 0.5–2.5 dm tall; stems initially several from the base, briefly decumbent and erect above, with age more spreading, decumbent, ascending distally, 1–3(–7) dm long, and the plants becoming bushy, the internodes (1.0–)2–4(–6.5) cm long, green, sometimes purple with age, 4-angled, obscurely grooved on two sides when young, moderately to strongly (below inflorescence) hirtellous to pilose with slender, tapering erect, mostly straight hairs 0.2–1.2(–1.4) mm long, sometimes with stipitate glands to 0.2 mm long below the inflorescence. Leaves opposite and in axillary clusters, broadly ovate to ovate-rhombic in outline, 11–25(–45) mm long, (6–)12–22(–26) mm wide, shorter than the internodes, with petioles 2–6 mm long, the blades 2–3 pinnatifid, deeply divided nearly to the midrib, the divisions variously revolute, oblong to lanceolate, 1–7 mm long, 0.8–1.5(–3.5) mm wide, with 7–28 ultimate, acute to obtuse lobes, the blades flat to usually conduplicate with the lobes ascend-



ing, with rather stiff, tapering unicellular hairs 0.2–0.5(–0.8) mm long on both surfaces, these generally dispersed and ascending on both surfaces, the hairs sometimes with pustulate bases, the veins impressed above, broadened beneath, the blades green to grayish due to the vestiture. Spikes terminal on all branches, 10–25(–35) mm long, 11–12 mm wide, densely crowded, the inflorescence axis seldom elongating at the base; peduncles 14–24 mm long, or the spikes closely subtended by leaves, the spike rachis ± pilose with hairs to 1.4 mm long and often with stipitate glands; bracts ascending, linear-lanceolate, 3.3–6.1 mm long, to 0.6–1 mm wide, hirsute along margins and midvein with hairs 0.2–1.1 mm long and with stipitate glands, 51–89 percent as long as the calyx; calyces initially 5–7 mm long, membranous between the 5 green veins, hirtellous and hirsute with hairs 0.2–0.8 mm long, usually with stipitate glands 0.1–0.2 mm long, the lobes unequal, 0.4–1.4 mm long, green or purple tipped, in fruit the calyces becoming truncated and to 1.5 mm broad at the base; corollas salverform, the tubes 6–7.5 mm long, expanding to 1.0–1.3 mm wide at the throat, the limbs white or tinged with lavender, (5.5–)6.0–9.0 mm wide, the 5 lobes all retuse, 1.6–3.5 mm long, 1.7–3.8 mm wide; the tube orifice with white or yellow moniliform hairs to 0.7 mm long; distal anterior anthers 0.6–0.8 mm long, the anther gland obscure or extending above the anthers, the filaments 0.5–0.7 mm long, the proximal posterior anthers 0.5–0.6 mm long, the filaments 0.2–0.3 mm long; style 5.5–6.2 mm long. Mature nutlets (2.0–)2.2–2.7 mm long, rounded at the tip, the central body 0.55–0.75 mm wide, the whitish commissural face 0.25–0.3(–0.35) mm wide, this rounded at the tip and extending to within 0.15–0.4 mm of the rounded nutlet tip, weakly aculeate with papillae to 0.1 mm long, the basal pericarp slightly expanded, hollow, 0.6–0.85 mm wide, the outer pericarp black, shallowly reticulate in the distal half, the reticulate pattern disorganizing into vertical striae in the lower half, the post-dehiscent receptacle yellowish, 4-angled, distinct.

Central trans-Pecos Texas (Fig. 3), mostly on limestone derived, calcareous soils, roadsides, mesquite flats, grasslands, with specimens verified from Brewster, Pecos, Hudspeth, Terrell and Reeves counties, Texas, flowering March and April, 2500–4000 ft. elevation. Moldenke 1964b sites additional specimens from Houston, Montgomery, Glasscock, Presidio, Val Verde, LaSalle counties, Texas, as well as San Miguel Co., New Mexico and the Mexican states of Coahuila and Nuevo León. His Montgomery Co., was from Stockton (= Ft. Stockton, Pecos Co., Tex.) His San Miguel Co., New Mexico was from Pecos Valley (= Pecos Co., Tex.) Others were *G. verecunda* or *G. pumila*.

The species has more strongly divided leaf blades, with the blade narrowed to 1/10 of the leaf width at the midvein, and sometimes have a denser vestiture. They have large corollas with tubes 6–7.5 mm long, and limbs 6.2–9.0 mm wide, and nutlets are shorter, rounded at the tip, not strongly expanded at the base, the commissural face is narrower than the nutlet width, and its distal surface is



rounded, not retuse, and the aculeae on the commissural face are reduced to only 0.1 mm in total length.

*Glandularia racemosa* is easily separated from *G. quadrangulata* and *G. verecunda*, as leaves are more deeply divided, often with a denser vestiture, the corolla limbs are larger, and the nutlets are much shorter, without a broadly outwardly flaring base, the commissural face is notably narrower than the central portion of the nutlet, and the distal portion of the commissural face is rounded, not retuse and occurs 0.15–0.3 below the rounded fruit tip. Umber (1977, 1979) notes relates this species to the *Glandularia bipinnatifida* complex, and reports hybridization between *G. racemosa* and *G. bipinnatifida* documented by mixed flavonoid profiles in the hybrids (Umber 1977).

A separate paper will deal with Turner's (1999) reclassification of the *Glandularia bipinnatifida* complex.

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